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7. The cells identified here are considered androgen-specific target cells because DHT is not converted to estrogen (*4*) and because prior injection of estradiol-17β (2 μg/100 g) does not reduce the nuclear uptake of labeled DHT [M. Sar and W. E. Stumpf, in *Abstracts, Fifth International Congress of Endocrinology* (Hamburg, 1976), p. 241]. Also, the distributions of cells with radioactivity concentrations after [^{3}H]estradiol or [^{3}H]DHT injection are not identical.
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15. Supported by PHS grants NS09914 and HD03110. We thank L. Patterson and S. Huang for technical assistance and P. Newell for preparation of drawings.

24 September 1976

Stereopsis in the Falcon

Abstract. *Stereoscopic depth perception is demonstrated in the falcon, a nonmammalian with binocular vision. This result complements recent physiological evidence for binocular interaction in the bird visual system, and suggests that stereopsis may be a general attribute of vertebrate vision and not an exclusive product of mammalian evolution.*

Binocular vision, present whenever an animal's eyes view a common segment of visual space, provides the horizontally disparate stimulation considered to be essential for the relative perception of depth known as stereopsis (*1, 2*). Stereopsis, known for more than 100 years to exist in humans, provides a compelling rationale for the evolution of mechanisms designed to promote binocularity, such as yoked eye movements and semidecussation of the optic tract, which are present in mammalian visual systems and are particularly well developed in primates. The apparent absence of these mechanisms in nonmammalians, which have independent eye movements and complete decussation of the optic tract, supports the hypothesis that binocular vision and the attendant capacity for stereopsis have been products of mammalian evolution and indeed may be defining characteristics of primates (*3–5*).

But recent neuroanatomical comparisons of the visual systems of mammals and nonmammals have revealed many similarities between the older vertebrate classes and the more recently evolved mammals (*6*). The bird visual system has received special scrutiny, and in the pigeon and the owl pathways have been identified that would permit extensive interaction between the eyes (*7, 8*)

We now report a behavioral demonstration of stereopsis in the falcon, a predatory nonmammalian with excellent acuity and with temporal foveae that provide binocular vision (*9, 10*). Our subject was an American kestrel (*Falco sparverius*), which was trained to select a stereoscopic form in a classic two-choice discrimination task. In this testing situation, the bird sits on a perch and views two displays enclosed in parallel alleys; flying to the correct display (the stereoscopic form) produces a food reward, flying to the incorrect display (no stereoscopic form) produces no reward. The position of the correct stimulus is varied randomly so that chance performance would be 50 percent correct; performance significantly above chance would be evidence of successful discrimination (*11*).

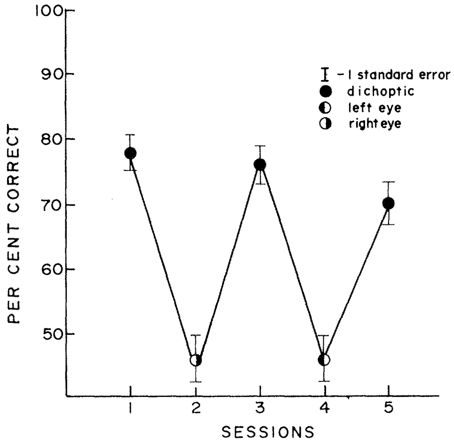

Fig. 1. Detection as a function of binocular and monocular viewing conditions. The binocular condition (●) refers to dichoptic or separate stimulation of each eye by the red and the green dot matrices. This is accomplished by placing red and green filters before the eyes and fulfills the requirement for stereoscopic presentation. The monocular conditions refer to stimulation of both eyes by only one dot matrix, either red or green. This is accomplished by placing filters of the same color, red or green, before the eyes. (◐) Stimulation by the left-eye matrix; (◑) stimulation by the right-eye matrix. The testing sessions, consisting of 25 trials each, were consecutive.

The essential element in testing for stereopsis in animals is a stereopsis display that contains no monocular cues an animal might exploit through such strategies as alternately closing the eyes or making lateral head movements to obtain motion parallax information. A display free of monocular cues is provided by random element stereograms in which the left and right eye segments each consist of a matrix of thousands of minute dots (*12*). Disparity is introduced by displacing a subset of dots in one matrix. When both segments are viewed by an observer with stereopsis, the visual system detects the disparity and generates the perception of a stereoscopic form that has distinct edges and a palpable surface. When each segment is viewed alone or both are viewed by an observer without stereopsis, no trace of the form is visible—only a matrix of randomly ordered dots can be seen. We used random element stereograms consisting of large matrices of red and green dots generated on a modified color television receiver. When appropriate red and green filters are placed before the eyes the red and green dot matrices stimulate separate eyes, thereby fulfilling the conditions of stereoscopic viewing (*13*).

The falcon was trained to fly in the testing apparatus while wearing a kind of helmet-goggle device that placed filters before its eyes. The filters completely covered the field of view so that it was not possible to view the display without looking through the filters. Through a gradual series of steps we trained the bird to fly to the display containing the stereoscopic form, which was a vertical rectangle (1° by 3°) appearing in depth in front of the display background (that is, crossed disparity). During the initial stages of training, discrimination was aided by nonstereopsis information about the location and shape of the form. In the final stage of training, only stereopsis information was available. The stereograms were in the dynamic mode, in which all elements of the matrices were replaced every 16 msec by a random generator. The replacement produces a scintillating apparent motion of the elements because the spatial positions of individual elements change, but the clarity, shape, and depth of the stereoscopic form are not altered. Replacement of elements on a random basis contributes to the elimination of potential nonstereopsis cues. It is possible that if the positions of all elements in the stereogram remained unchanged and were examined for thousands of trials, some feature of the element pattern could be remembered and used for successful discrimination. But that possibility is rather improbable when the pattern of elements is changed randomly 62 times per second.

We found that the bird could reliably select the display containing the stereoscopic form (on the order of 80 percent correct), and this in itself is very strong evidence that the bird possesses stereopsis. But we carried out additional experiments to test more stringently for stereopsis and to explore some of its characteristics.

One standard test for stereopsis is to measure performance under monocular viewing conditions, since stereopsis requires the simultaneous interaction of both eyes. Since the bird would not fly with one eye occluded, we carried out the equivalent of monocular occlusion by placing filters of the same color before the bird's eyes. This procedure permits only one dot matrix to stimulate the eyes. These monocular control sessions were introduced several times during testing. Typical results are shown in Fig. 1, where it can be seen that discrimination falls to chance when the eye filters are of the same color.

To obtain an estimate of the bird's threshold for stereopsis, we varied disparity in discrete steps over sessions. A session where discrimination was difficult was followed by a session where discrimination was easy, in order to maintain motivation. Figure 2 shows how performance varied with disparity. Note that performance declines at the largest disparities; human observers reported the loss of stereopsis at these disparities, presumably because some fusion limit had been exceeded. Performance as a function of disparity cannot be directly compared with that of humans, but the data do suggest that the falcon is sensitive to the same order of magnitude of disparity as humans (*14*).

Perhaps the bird was responding to "something" in depth rather than to the configuration of the stereoscopic form. If so, then a change in configuration would not alter performance. But if the configuration or shape of the stereoscopic form was being used by the bird to make correct discriminations, a change in configuration would initially impair discrimination because of negative transfer. To test the sensitivity of the bird to configuration, we rotated the stereoscopic form by 90°. The result of this change, shown in Fig. 3, reveals that performance abruptly falls on introduction of the horizontal rectangle and then gradually improves with repeated exposure. This disruption in performance strongly suggests that the bird responded not only to the depth of the stereoscopic form but also to its configuration.

Together the results lead us to conclude that the falcon possesses stereopsis, a conclusion that complements nicely the physiological evidence for binocular interaction within the bird's visual system. Moreover, the perception of stereopsis from random element stereograms is considered to require more complex neural processing than perception of stereopsis from displacement of discrete contours (*15*).

The fact that at least one nonmammalian possesses stereopsis invites the speculation that many nonmammalians representing different lines of descent and possessing anatomical features that favor binocular vision, such as temporal foveae, prismatic corneas, and sighting grooves, may also have stereopsis. Perhaps stereopsis is not an emergent capacity bestowed on a relatively small number of elite animals but is a fundamental attribute of vertebrate vision.

One implication of that speculation, if it is correct, is that the breadth of animals that can be used to investigate anomalies of binocular vision in humans, such as strabismic amblyopia, can be expanded; such an expansion would permit novel inquiry into the mechanisms underlying binocular vision and stereopsis (*16*).

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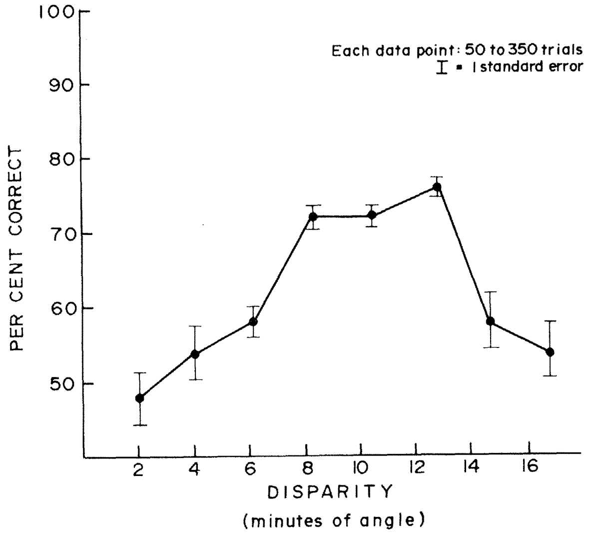

Fig. 2. Detection as a function of increasing disparity. The eight disparity values are the ones the system could generate, as described in (*14*); the disparity direction is crossed—that is, the stereoscopic form appears to lie in front of the background and the apparent distance between form and background increases with increasing disparity. The variable number of trials at each data point is a by-product of the testing procedure, wherein difficult discrimination sessions were followed by easy discriminations in order to maintain motiviation.

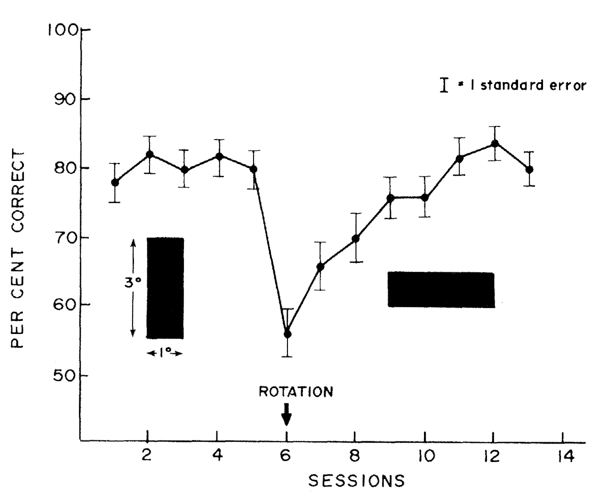

Fig. 3. Detection as a function of change in configuration of the stereoscopic form. At the start of session 6 the vertical rectangle was rotated 90° to the horizontal position, thus providing a change in the stimulus never previously introduced during training and testing. The sessions, each consisting of 25 trials, were consecutive.

References and Notes

1. C. Wheatstone [*Philos. Trans. R. Soc. London* **128**, 371 (1938)] showed that the slightly disparate stimulation provided by horizontally separated eyes (that is, retinal disparity) is a sufficient condition for producing stereopsis. Since Wheatstone's discovery, stereoscopic depth perception in humans has been the topic of an intensive systematic inquiry, which has resulted

in a quantitative descriptive theory of the variables responsible for stereopsis. Reviews and discussions of this work can be found in H. Helmholtz [*Physiological Optics* (Optical Society of America, Washington, D.C., 1925; Dover, New York, 1962)], K. N. Ogle [in *The Eye*, H. Davson, Ed. (Academic Press, New York, 1962), vol. 4, pp. 271–417], B. Julesz (*2*), and W. L. Gulick and R. B. Lawson [*Human Stereopsis: A Psychophysical Analysis* (Oxford Univ. Press, London, 1976)].

2. B. Julesz, *Foundations of Cyclopean Perception* (Univ. of Chicago Press, Chicago, 1971).
3. The emergence of binocularity during the course of mammalian evolution has attracted considerable attention, and several hypotheses have been advanced to account for it [see, for example, G. E. Smith, *The Evolution of Man* (Oxford Univ. Press, London, 1924); G. L. Walls (*4*); S. Polyak (*5*); W. E. LeGros Clark, *Antecedents of Man* (Edinburgh Univ. Press, Edinburgh, 1959); M. Cartmill, in *The Functional and Evolutionary Biology of Primates*, R. H. Tuttle, Ed. (Aldine-Atherton, Chicago, 1972), pp. 97–122]. Only recently, however, has the assumption been confirmed that stereopsis is present in animals other than humans. R. Fox and R. Blake [*Nature (London)* **233**, 55 (1971)], J. Packwood and B. Gordon [*J. Neurophysiol.* **38**, 1485 (1975)], and R. Blake and H. V. B. Hirsch [*Science* **190**, 1114 (1975)] have found behavioral evidence for stereopsis in the cat. E. W. Bough [*Nature (London)* **225**, 42 (1970)], R. F. Sarmiento [*Vision Res.* **15**, 493 (1975)], and A. Cowey, A. M. Parkinson, and L. Warnick [*Q. J. Exp. Psychol.* **27**, 93 (1975)] have found behavioral evidence for stereopsis in the rhesus monkey. These data complement recent neurophysiological investigations that have revealed cortical neurons in cat and in monkey that respond optimally to retinally disparate stimuli [see, for example, H. B. Barlow, C. Blakemore, J. D. Pettigrew, *J. Physiol. (London)* **193**, 327 (1967); P. O. Bishop, in *The Neurosciences: Second Study Program*, F. O. Schmitt, Ed. (Rockefeller Univ. Press, New York, 1970), pp. 471–485; D. H. Hubel and T. N. Wiesel, *Nature (London)* **225**, 41 (1970)].
4. G. L. Walls, *The Vertebrate Eye* (Cranbrook Institute of Science, Bloomfield Hills, Mich. 1942).
5. S. Polyak, *The Vertebrate Visual System* (Univ. of Chicago Press, Chicago, 1957).
6. See, for example, the symposium edited by D. Ingle and G. E. Schneider, *Brain Behav. Evol.* **3** (Nos. 1–4), pp. 1–352 (1970); D. Ingle, *Science* **181**, 1053 (1973); W. C. Hall, *Brain Behav. Evol.* **5**, 95 (1972); T. A. Duff and S. O. E. Ebbesson, *Science* **182**, 492 (1973); H. B. Sarnat and M. G. Netsky, *Evolution of the Nervous System* (Oxford Univ. Press, London, 1974).
7. Neuroanatomical investigations by Karten and colleagues [for example, H. J. Karten, W. Hodos, W. J. H. Nauta, A. M. Revzin, *J. Comp. Neurol.* **150**, 253 (1973)] have revealed many structures and pathways in the avian visual system that seem to be analogous to those in the mammalian visual system. In the bird telencephalon a region known as the visual Wulst receives extensive input from both eyes and appears to be an analog of the visual cortex in mammals. Pettigrew and Konishi (*8*) have recorded from single neurons located within the Wulst of the owl and found neurons optimally responsive to disparate binocular stimuli.
8. J. D. Pettigrew and M. Konishi, *Science* **193**, 675 (1976).
9. Behavioral tests of kestrel acuity revealed that it exceeds human acuity by a factor of 2.6 (*10*), a result consistent with estimates of falcon and hawk acuity derived from optical characteristics of the eye [R. Shlaer, *Science* **176**, 922 (1972)] and from the anatomy of the retina [K. V. Fite and S. Rosenfield-Wessels, *Brain Behav. Evol.* **12**, 97 (1975)]. The retinas of falcons and hawks have a well-developed temporal fovea in addition to a central fovea; the lateral position of the temporal fovea provides binocular overlap [Walls (*4*), Polyak (*5*), Fite and Rosenfield-Wessels (above)].
10. R. Fox, S. W. Lehmkuhle, D. H. Westendorf, *Science* **192**, 263 (1976).
11. The two-choice discrimination task we used is very similar to the one described in our prior investigation of kestrel acuity (*10*). The bird learns to fly from the starting perch to a perch located below each stimulus display. The distance between the starting perch and the stimulus perch is 168 cm. The weight of the bird landing on the correct perch triggers the reward delivery system, which exposes a small cup containing a morsel of beef heart that can be seized by the bird's beak. If the bird lands on the incorrect perch the cup is not exposed and the stimulus display and other illumination in the alley is turned off briefly. Training to perform in the test apparatus is accomplished by gradually shaping behavior, following the tenets of operant conditioning, with food as the reward. The bird, weighed daily before and after testing sessions, was maintained in excellent health at an average weight of 100 g. All the bird's daily food ration was earned in two daily training-testing sessions of 20 to 25 trials, one session in the morning and one in the afternoon. Since beef heart does not satisfy all the bird's digestive and nutritive requirements, it was fed a mouse once a week.
12. Random element stereograms [developed and systematically investigated by B. Julesz; see, for example, *Bell Syst. Tech. J.* **39**, 1125 (1960) and (*2*)] produce compelling stereoscopic depth percepts in the absence of monocularly discernible contours.
13. The technique of dichoptic stimulation through color separation, the anaglyph method, is well known [see, for example, Y. LeGrand, *Form and Space Vision* (Indiana Univ. Press, Bloomington, 1967); R. S. Woodworth, *Experimental Psychology* (Holt, New York, 1938)]. We have found that Wratten filters 29 (red) and 58 (green) provide acceptable color separation for the red and green colors produced by most modern color television receivers. The system we used for generating stereograms consisted of an electronic device that controlled the sweep and on-time of the red and green electron guns of a color television receiver. A large number of red dots and green dots, produced by a random generator, appeared to be continuously present on the screen (physically, a new dot pattern was generated every 16 msec, the time required for one scan of the cathode-ray tube). Disparity was introduced by delaying the on-time of one of the guns at predetermined points during the scan. Variations in disparity magnitude and configuration of the stereoscopic form could be introduced. The device controlled two identical television receivers (Hitachi model 100-C), one for each alley of the testing apparatus; from the starting perch the display portion of each receiver was 4.4° by 6.2°. The stereoscopic form could be generated on either one of the receivers at the option of the experimenter.
14. The abscissa of Fig. 2 indicates the eight disparities that could be generated by the display system. The disparities are derived, with appropriate correction for bird interpupillary distance, from the formula used for calculating disparity induced by discrete, monocularly visible contours [C. H. Graham, in *Handbook of Experimental Psychology*, S. S. Stevens, Ed. (Wiley, New York, 1951), pp. 868–920]. While it was not possible to compare human performance with falcon performance under comparable conditions, we did ask humans to report on the magnitude of perceived depth induced by the eight disparities. With their heads located adjacent to the starting perch they estimated, in arbitrary units, how far in front of the background the vertical rectangle appeared. For the first six disparities perceived depth increased. For the two largest disparities it become difficult to maintain the depth percept. Some observers reported that the rectangle no longer appeared in depth but lay in the same plane as the background. This difficulty with the larger disparities parallels the decrement in performance exhibited by the falcon for the same disparities. These observations suggest to us that there are no dramatic differences in the range of disparities to which falcon and human are sensitive.
15. Stereopsis by discrete contours has been called local stereopsis, while stereopsis by random element stereograms has been called global stereopsis. See Julesz (*2*) and P. O. Bishop and G. H. Henry [*Annu. Rev. Psychol.* **22**, 119 (1971)] for a discussion of the distinction between local and global stereopsis.
16. Since many nonmammalians are oviparous, sophisticated techniques derived from embryological research might be used to investigate the development of the binocular visual system. In this regard, Pettigrew and Konishi (*8*) report that early experience influences the development of binocular vision in owls.
17. We thank the Tennessee Wildlife Resources Agency and the U.S. Fish and Wildlife Service for the excellent cooperation extended to us. The work was authorized by state scientific collectors permit No. 516 and federal scientific collectors permit PRT-7-01-C-Z-NV. Support was provided by NIH grant EY00931.

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Homosexual Rape and Sexual Selection in Acanthocephalan Worms

Abstract. *Acanthocephalan males have cement glands associated with the vas deferens, secretions from which seal the female vagina with a cap after copulation and so prevent subsequent insemination. Homosexual rape results in the male victim having the genital region sealed off with cement and effectively removed from the reproductive population. Sperm and cement are transferred to females during copulation, but apparently only cement is transferred to males during homosexual rape. Acanthocephalans conform to a parental investment model, and we interpret the evolution of the cement gland and sexual behavior as the result of sexual selection.*

Rape occurs in a variety of circumstances, but in nonhumans it usually is related to male reproductive success. In some species of *Drosophila*, males are able to rape females that have already copulated (*1*). The sperm of the rapist, since it is the last insemination, is then packed into the seminal receptacle on top and is used first by the female fertilizing a majority of the eggs (*2*). In the rhabdocoel turbellarian *Stenostomum oesophagium*, behavior has been reported (*3*) that we interpret as rape. Individuals are nonselfing hermaphrodites, and cross-fertilization occurs; but individuals will approach quiescent individuals and rapidly evert the penis, hypodermically impregnating the quiescent individual without allowing cross-fertilization. There are other reports (*4*) of this sort of behavior among turbellarians, suggesting that individuals will promiscuously inseminate but selectively allow themselves to be inseminated. After homosexual rape in the anthocorid bug *Xylocaris maculipennis*, the sperm of the rapist enters the vas deferens of the victim and is used by the victim during copulation. An individual may be raped even while he is copulating with a female (*5*). We report here homosexual rape in the acanthocephalan worm *Moniliformis dubius* and interpret this behavior and other aspects of the biology of acanthocephalans in the context of parental investment and sexual selection.